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Ants of the Genus Formica from the Baltic Amber

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ABSTRACT: Baltic Amber material in the Institute of Paleontology, USSR Academy of Sciences was studied, yielding 4 new species of Formica. One, F. (Proformica) proformicoides Dlusskiy represents a new subgenus which Dlusskiy considers likely to be the morphological prototype of the tribe Formicini. Keys to Baltic Amber species and descriptions of 4 new species are presented. Morphological and behavioral relationships among the Formicini are given. -- R. W. Hodges.

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In the past only five species of the genus Formica have been known from the Baltic Amber. One of these, F. flori, was described by Mayr (in 1868), the rest by Wheeler (in 1915) in a monograph on the ants of the Baltic Amber. The present author has worked over part of the Amber collection in the Institute of Paleontology of the USSR Academy of Sciences. The material turned out to contain a number of new ant species, including four belonging to Formica. One of these, F. proformicoides, is of very great interest, since it combines features of the morphologically most primitive members of the genera Formica, Proformica and Cataglyphis and is probably the morphological prototype of the Formicini tribe. These new data make it possible to give a more complete review of the genus than Wheeler was able to do in his monograph.

KEY TO SPECIES OF GENUS FORMICA FROM THE BALTIC AMBER (BASED ON WORKERS)

1 (2) Maxillary palps elongate, reaching the occipital foramen; 4th segment 1.5 times as long as long as the 5th (fig. 2f), flagellar segments abbreviate (fig. 2j). Thorax, limbs and inferior side of head without erect hairs. Length about 4 mm . . . . . F. (Protoformica) proformicoides, sp. nov.

2 (1) Maxillary palps not reaching occipital foramen; 4th and 5th segments roughly equal (fig. 2d); flagellar segments elongate . . . . . 3.

3 (4) Entire body, including legs and pedicel clothed in abundant, erect hairs. Pedicel straight, even at the base. Length 3.5-4.5 mm . . . . . F. (? Serviformica) horrida Wheeler, 1915.

4 (3) Legs and pedicel, and often also the thorax without erect hairs. Pedicel slightly curved (fig. 1, a-c) . . . . . 5.

5 (6) Erect hairs present only at the apex of the abdomen. Maxillary palps short, reaching only midway from the mouth to the occipital foramen. Abdomen with abundant, recumbent hairs. Length 9 mm . . . . . F. (F.) clymene Wheeler, 1915.

6 (5) Erect hairs present, at least over the whole abdominal surface, on the superior side of the head and on the coxae . . . . . 7.

7 (8) Thorax elongate, with deep, wide, selliform incision between the mesonotum and epinotum (fig. 1d), as in Prenolepis. Thorax with numerous erect hairs. Length 7.5 mm . . . . . F. (? Serviformica) strangulata Wheeler, 1915.

8 (7) Thorax flat or slightly extended, but not so much as in the preceding species. Depression between mesonotum and epinotum narrow and deep (fig. 1a and b) . . . . . 9.

9 (10) Large forms, about 10 mm long. Build flat, as in Formica s. s. Epinotum circular in profile. The whole body, except the limbs, abundantly clothed in erect hairs. Maxillary palps short, reaching only midway from the mouth to the occipital foramen. Recumbent pubescence abundant . . . . . F. (F.) phaethusa Wheeler, 1915.

10 (9) Smaller, 4.5-7 mm long. Superior side of the head with sparse, erect hairs (one pair on the frons, one or more pairs in the ocellar region, and several pairs on the clypeus). On the thorax erect hairs present only on the pronotum. Maxillary palps extend beyond midway from the mouth to the occipital foramen . . . . . 11.

11 (12) Recumbent pubescence abundant; on the abdomen the length of the recumbent hairs is much greater than the distance between them. Body mat. Epinotum angulose in profile . . . . . F. (Serviformica) flori Mayr, 1868.

12 (11) Recumbent pubescence found: length of recumbent hairs on abdomen equal to less than the distance between them. Body shiny. Epinotum circular in profile . . . . . 13.

13 (14) On the underside of the head a pair of erect hairs. On top of the thorax no erect hairs. Dis-

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tinct depression visible in profile between the pronotum and the epinotum (fig. 1a) . . . . . F. (Serviformica) baltica, sp. nov.

14 (13) No erect hairs on underside of head. Three pairs of erect hairs on pronotum. Recess between pronotum and mesonotum almost imperceptible (fig. 1b) . . . . . F. (Serviformica) antiqua, sp. nov.

Genus Formica Linnaeus, 1758

Subgenus Serviformica Forel, 1913

Formica (Serviformica) baltica Dlussky, sp. nov.

Holotype. PIN No. 364/407; Baltic Amber.

Description (fig. 1a). Worker. Build compact. Head with rounded occipital margin, its length slightly greater than its width. Clypeus with slightly acuminate anterior margin and with carina. Frontal area distinct. Eyes large. Pedicel longer than head without mandible. Flagellar segments elongate, the first the longest, 1.2 times as long as the 2nd or 3rd, which are of equal length; length of 1st segment 2.4 times its width, length of 2nd and 3rd segments 2 times as long as their width. Mesothorax in profile sharply divided from the prothorax and rising above it at a protruding angle. Epinotum rounded in profile its basal surface roughly equal to the sloping surface. Squamella thick: its anterior surface convex, its posterior surface flat, its superior margin without cristae, rounded if viewed from behind.

The whole body, except for the abdomen, covered with fine, surface sculpture; abdomen glabrous, except for the hair punctures. Structure of frontal area not visible.

Erect hairs present on head in the ocellar region (one pair), on the frons (one pair), on the clypeus (4 pairs) and on the underside of the head (one pair). On the fore femora, along the inner margin, there is a row of 3 or 4 hairs; middle and hind femora without erect hairs. No erect hairs on any of the tibiae, but spinules present along the inner margin. Thorax and squamella without erect hairs. Abdomen with sparse, erect hairs present over the whole surface of tergites and on all the sternites. Sloping surface of 1st tergite without erect hairs.

Recumbent pubescence on head, thorax and limbs, small and fine, but very abundant. On the abdomen the recumbent pubescence is sparse, the length of the hairs being equal to or less than the distance between them.

Dimensions, mm, Holotype No. 364/407: body length 5.5; length of thorax 2.1; length of head without mandible 1.5.

Comparison. In structure of head and thorax and in the proportions of the antennae (group characters) F. (S.) baltica is very similar to the living species F. (S.) gagates Latr., which is a species apart in the subgenus Serviformica, but the fossil species can be readily distinguished from the living species by the character of their chaetotaxy and recumbent pubescence (specific characters) and by their considerably smaller size.

Geologic and geographic range. Baltic Amber.

Material. Holotype and Spec. No. 364/366. The second specimen is interesting in that it holds the head of a species of Camponotus in its jaws.

Formica (Serviformica) antiqua Dlussky, sp. nov.

Holotype. PIN No. 364/419; Baltic Amber.

Description (fig. 1b, c). Worker. Structure of head and antennae as in F. (S.) baltica. Thorax flat; mesonotum very much rounded in profile in contrast to F. baltica. Squamella also more rounded in profile and not so abruptly constricted towards the apex.

Erect hairs on the top of the head, as in F. (S.) baltica. Three pairs of erect hairs on the prothorax. No erect hairs on the underside of the head. Row of erect hairs on the inner margin of fore- and mid-femora. One hair at the base on the inner surface of the hind femora. Chaetotaxy on the abdomen more abundant than in F. (S.) baltica. Recumbent pubescence as in F. (S.) baltica.

Dimensions, mm, Holotype No. 364/419: Length of thorax 1.75; length of head without mandible 1.17; width of head below eyes 1.10; length of pedicel 1.45.

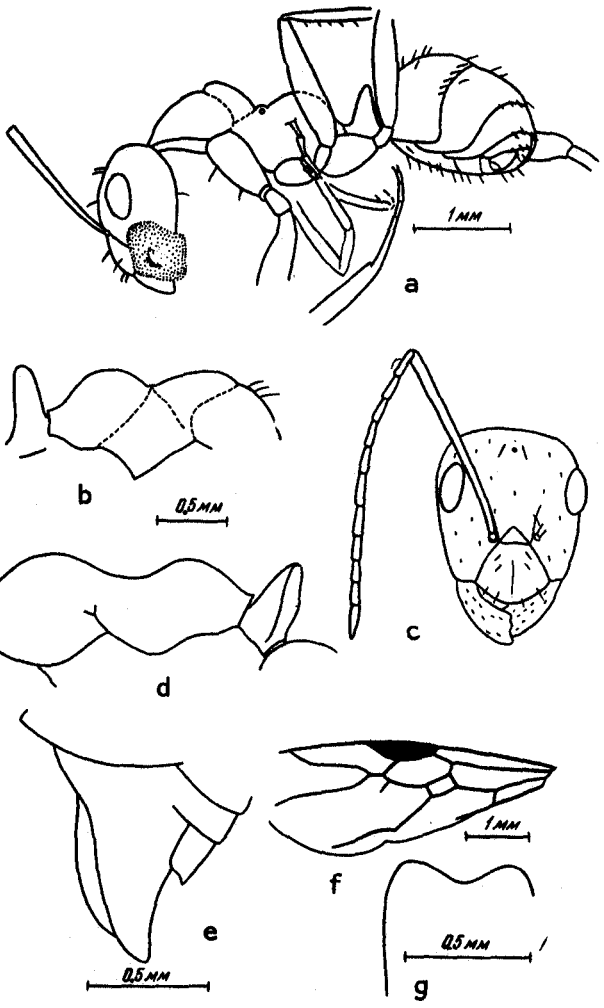

FIGURE 1. Members of genus Formica.

a - F. (Serviformica) baltica sp. nov.; Holotype No. 364/407, worker;
b, c - F. (Serviformica) antiqua sp. nov.; Holotype No. 364/419, worker: b - thorax and squamella in profile; c - head from above;
d - F. (? Serviformica) strangulata Wheeler, thorax and squamella in profile;
e-g - F. (? Serviformica) parvula sp. nov.; Holotype No. 364/-414, male: e - genitalia; f - forewing; g - squamella from in front.

Comparison. This species is very close to F. (S.) baltica, but differs in the shape of the mesonotum and the arrangement of the erect hairs. Like the preceding species it belongs to the group F. (S.) gagates.

Comment. The group F. (S.) gagates, at present represented by only one species, was probably more diversified in the past and comprised several species.

Geologic and geographic range. Baltic Amber.

Material. Holotype. Almost the entire body covered with fine, yellowish pruinescence, so that it is impossible to discern the body sculpture.

Formica (? Serviformica) parvula Dlussky, sp. nov.

Holotype. PIN No. 364/414; Baltic Amber.

Description (fig. 1, e-g). Male. Squamella thick in profile, with broad, rounded incision in in superior margin. Shape of abdomen, structure of genitalia and wing venation same as those of living members of the subgenus Serviformica. Body abundantly covered with microscopic, recumbent hairs. Erect hairs present only on the abdominal sternites and the genitalia.

Dimensions: Length of hind femur 0.84 mm.

Comparison. The new species differs from all known species of the F. (S.) fusca group in lacking erect hairs on the upper side of the abdomen and in regard to this character it approaches living members of the F. (Coptoformica) pressilabris group; but nothing definite can be said until a better preserved specimen is found.

Comment. Until now the male of only one fossil species of the genus had been known, F. (S.) flori Mayr, which is very similar to the male of the living species F. (S.) lemani Bondr. (Yarrow, 1954). Of all living members of the F. (S.) fusca group, F. (S.) fusca L. has the least developed chaetotaxy, but even in that species there are erect hairs on the posterior margin of the last 2 or 3 tergites. The remaining species, including F. (S.) lemani, have numerous erect hairs on the superior margin of the squamella.

To judge from the correlations observable in the living species, F. (? S.) parvula must be the male of a species in which the workers have extremely little direct pubescence and the body length is of the order of 4-7 mm, small for Formica.

Geologic and geographic range. Baltic Amber.

Material. Holotype. Specimen in poor condition, consisting of the abdomen with the genitalia, the petiolus, the left pair of wings and the middle and hind legs.

Subgenus Protoformica Dlussky, subgen. nov.

Type species. F. (Protoformica) proformicoides sp. nov., Baltic Amber.

Description (fig. 2). Worker. Head elongate, occipital margin without emargination. Anterior margin of clypeus without incision. Pedicel not long, 1/3 of it protruding beyond the occipital margin of the head. Flagellar segments abbreviate (fig. 2j). Maxillary palps elongate (fig. 2f), reaching the occipital margin; 4th segment 1.5 times as long as the 5th. Apical and pre-apical mandibular teeth elongate and partially fused, but the apical tooth almost twice as large as the pre-apical (fig. 2c). Frontal area distinct. Frontal ridges divergent (fig. 2b). Thorax gracile, with the typical Formica structure (fig. 2a). Macrochaetae lacking on anterior margin of clypeus and on mentum. Epinotal spiracles circular.

Species composition. Only the type species from the Baltic Amber.

Comparison. This species is distinguished from all subgenera of Formica by the elongate maxillary palps, the 4th segment of which is half as long again as the 5th, and, in addition, by the elongate apical and pre-apical mandibular teeth.

Comment. In a whole series of characters Protoformica occupies a quasicentral position among the forms Formica, Proformica and Cataglyphis. The mandibular structure, for example, is intermediate between that of Formica, in which the apical teeth are only slightly enlarged, and Proformica and Cataglyphis, in which the apical tooth is much longer than the rest. The Protoformica flagellum (fig. 2j) has the same structure as in Proformica (fig. 2k), but not the same as in the majority of Formica species (fig. 2i), for in this respect it resembles only Nearctic species of the F. neogagates Em. group. The maxillary palps in Protoformica (fig. 2f) are very similar to those of the primitive Cataglyphis (fig. 2g), although the latter are more elongate. In the specialized forms of Cataglyphis (fig. 2h) the palps are more elongate and the 4th segment is twice the length of the 5th. In all species of Formica (fig. 2d) and Proformica[1] (fig. 2e), the maxillary palps do not, as a rule, reach the occipital foramen and the 4th segment is roughly equal to the 5th.

All these morphological features of the new subgenus support the hypothesis of the subgenus being the morphological prototype of the Formicini tribe. What we see in the genus Formica is a tendency

[1] An exception is Proformica deserta K.-Ug., which should probably be regarded as an independent genus or assigned to Cataglyphis.

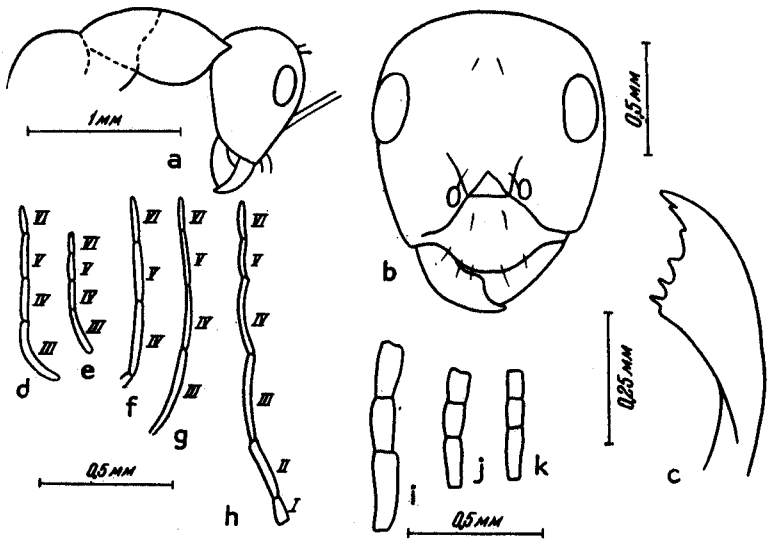

FIGURE 2. Some species of the tribe Formicini.

Formica (Protoformica) proformicoides sp. nov.; Holotype No. 364/371, worker: a - head and thorax in profile; b - head from above; c - mandible; f - maxillary palps; j - 1st 3 flagellar segments.

Formica (Serviformica) fusca Linnaeus: d - maxillary palps; i - 1st 3 flagellar segments.

Proformica epinotalis Kuznetsov-Ugamskiy: e - maxillary palp; k - 1st 3 flagellar segments.

Cataglyphis pallida Mayr: g - maxillary palp.

Cataglyphis flavigastra Karaw.: h - maxillary palp. (Roman figures indicate ordinal numbers of segments.)

toward abbreviation of the maxillary palps, a tendency carried to its extreme in the living group F. (Coptoformica) pressilabris and the fossil forms F. clymene and F. pfaethusa, which probably belong to the subgenus Formica s. s. In Cataglyphis, on the other hand, there is a pronounced tendency towards elongation and specialization of this organ, carried to the extreme in the most specialized members of the genus. However, the structure of the maxillary palps in the morphologically most primitive groups of both genera (the subgenus Serviformica of the genus Formica and the primitive members of Cataglyphis, for example C. pallida Mayr) is closest to that of Protoformica. Nor is there any doubt that characters such as the emargination of the occipital margin in Coptoformica and Rossomyrmex, the disappearance of the sutures of the frontal area in Proformica, the abbreviation (in Rossomyrmex) and considerable elongation (in a number of Cataglyphis and Neoformica forms) of the pedicel, the enlargement of the terminal mandibular tooth in Proformica or the loss of the teeth in Rossomyrmex and Polyergus, and the elongation of the thorax in Cataglyphis are all secondary effects, due to the specialization of these groups.

It should not be thought, of course, that Protoformica was the direct ancestor of the living Formicini, since highly specialized forms of the type F. (F.) clymene, F. (F.) phaethusa and Cataglyphus constrictus[2] have been found along with them in the Amber.

Formica (Protoformica) proformicoides Dlussky, sp. nov.

Holotype. PIN No. 364/371; Baltic Amber.

Description (fig. 2 a-c, f, j). Worker. Length of head somewhat greater than width, sides

[2]To judge from the drawing in Wheeler's monograph (1915), Formica constricta, described by Mayr (1868) as Camponotus constrictus, must be assigned to the genus Cataglyphis.

rounded. Length of pedicel slightly greater than length of the head without the mandibles. Flagellar segments short and thickened; length of the 1st segment 1.5 times as long as the 2nd and 2.8 times as long as it is wide; length of 2nd and 3rd segments, which are equal to each other, 1.8 times the width. Anterior margin of clypeus damaged, so that its shape is difficult to make out, but it can be seen that there is no emargination. Ratio of last maxillary palp segments – IV:V:VI = 1.5:1:1.

Thorax gracile. Inconspicuous depression between the pronotum and the mesonotum. Epinotum rounded in profile, its basal surface shorter than its sloping surface (fig. 2a). Squamella and abdominal tergites not visible.

Superior side of head glabrous and shiny, without conspicuous sculpture or recumbent pubescence. Mandibles with fine, longitudinal rugulae. Legs with fine surface sculpture. Thoracic and abdominal sculpture not visible.

Erect hairs present on head: on frons (one pair), in the ocellar region (one pair) and on the clypeus (one pair at the base and a series of slender hairs along the anterior margin). Thorax, underside of head and limbs without erect hairs. Spinules short, thick on the inside of the tibiae, not forming a complete row; spinules present only on apices of middle and hind tibiae. Erect hairs visible on the last abdominal sternites.

Dimensions, mm, Holotype No. 364/371: Length of thorax 1.5; length of head without mandibles 1.05; width of head below eyes 0.96.

Geologic and geographic range. Baltic Amber.

Material. Holotype. Head and limbs distinctly visible, thorax covered with a fine, white pruinescence, making it impossible to distinguish the sculpture and the recumbent pubescence; squamella, all tergites and 1st abdominal sternites not visible.

* * * * *

We can thus see that the Tertiary fauna of the genus Formica was fairly diversified. The incompleteness of previous studies is shown by the mere fact that although the myrmecologists have found and studied more than a thousand specimens of Formica, most of them (1,310 specimens), according to Wheeler (1915), belong to F. (S.) flori, whereas only one or two specimens of the remaining species have been found.

I have attempted to present my ideas about the phylogenetic links within the Formicini tribe, particularly in the genus Formica, and to determine the place of the Tertiary species found in the Baltic Amber within this system (fig. 3).

The Formicini tribe consists of 5 Recent genera and one fossil genus. Three of them (the living parasitic genera Polyergus and Rossomyrmex and the fossil genus Glaphyromyrmex found in the Baltic Amber and represented by one species, G. oligocenicus Wheeler) deviate so much from the common type that it is at the moment difficult to picture their phylogenetic connections. The other 3 genera (Formica, Proformica and Cataglyphus) form a more or less compact group. Within this group the most specialized is the genus Cataglyphis. In all probability this specialization was connected with the transition to existence under arid conditions. At present all species of the genus are typical inhabitants of the steppes, semi-deserts and deserts of Europe, Asia and Africa. The slender body and the elongate limbs permit very rapid movement (these ants are among the fastest-moving insects) and cover great distances in the search for food. The macrochaetae on the anterior margin of the clypeus and on the mentum and the elongate maxillary palps enable them to burrow passages in the dry sypuchka.[3]

This genus was evidently the first to break away from the common trunk (1).[4] A specialized member of the genus, C. constrictus Mayr, has been found in the Baltic Amber.

The separation of the genus Proformica (2) was also connected with the transition to life under a arid conditions. The living members of Proformica are steppe and semi-desert dwellers. Like the species of the genus Cataglyphis they are very mobile insects, but their specialization does not go so far as that of Cataglyphis. A characteristic feature of the majority of Proformica species is the

[3] Loose, fine-grained sand. -- Transl.

[4] Figures in parentheses correspond to figures in Figure 3.

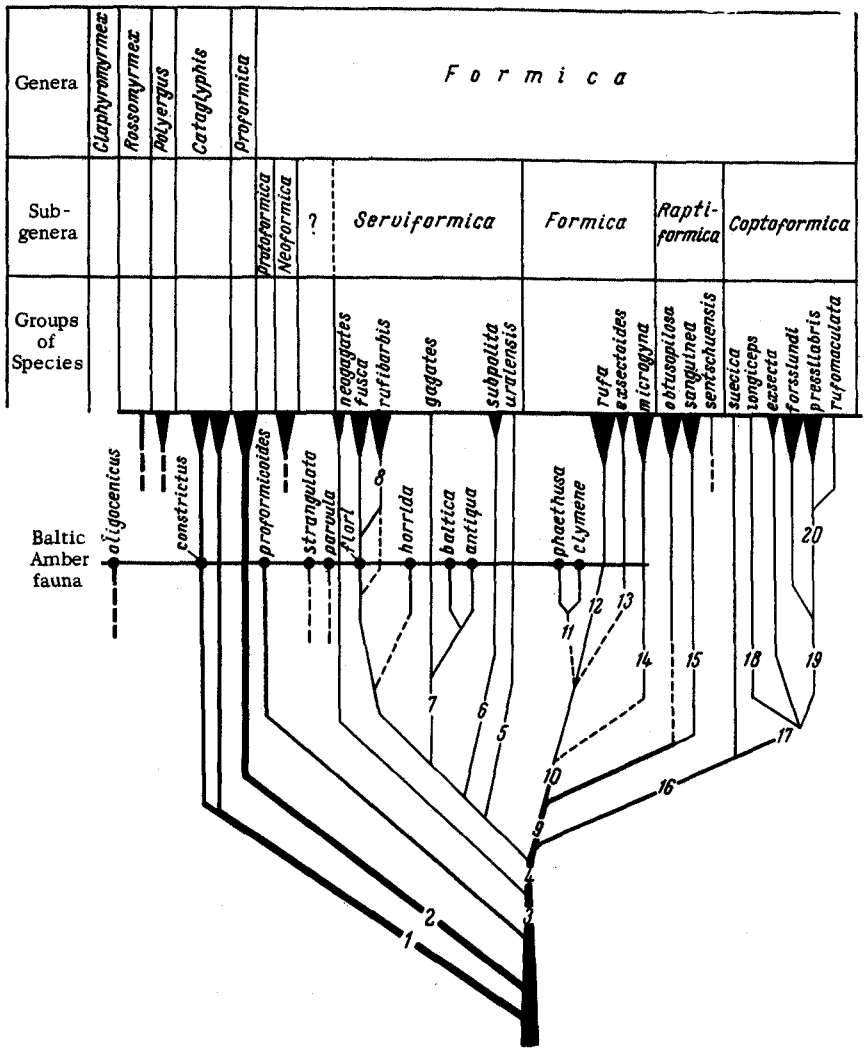

FIGURE 3. System of phylogenetic relationships within the Formicini tribe.

existence of a cast of "honey-storers," large workers in which the food reserves are stored, permitting the ants to survive adverse conditions in the nests.

As we have seen above, the most primitive subgenus of Formica is Protoformica. This is evidently the oldest subgenus. The abbreviation of the maxillary palps (3) and the elongation of the flagellar segments (4) in the remaining members of Formica took place after it had separated off. The subgenus Serviformica developed. This subgenus has until now been regarded as the oldest and most primitive member of Formica, while F. (S.) fusca L. has been regarded as the morphological prototype of the Formicini tribe (Wheeler, 1910 and others).

Even before the Tertiary period several groups of species broke away from this subgenus. In the ancestors of F. (S.) uralensis Ruzs. polymorphism of the workers appeared and the nest-building instinct became more complicated. These ants started to construct nests of plant residues (5). Polymorphism developed independently also in the Nearctic group F. (S.) subpolita. Antennae with very elongate flagellar palps, twice as long as their width, are characteristic of species belonging to the group F. (C.) gagates (7). In the Baltic Amber this group is represented by 2 species, F. (S.) baltica sp. nov. and F. antiqua sp. nov.

Wheeler (1910) wrote that F. (S.) flori Mayr, common in the Baltic Amber, is indistinguishable from the living F. (S.) fusca. But here he was treating F. (S.) fusca in a very wide sense, to include

not only the related species which he described later, but also certain species belonging to other groups (for example F. (S.) cunicularia Latr. or F. (S.) japonica Motsch), which he regarded as varieties of F. (S.) fusca. Yarrow (1954), after studying the male of F. (S.) flori, reached the conclusion that it was much closer to F. (S.) lemani Bondr. than to F. (S.) fusca. Unfortunately it is no longer possible to inspect the huge series of 1,310 specimens which Wheeler studied in the Konigsberg Museum. It is quite possible that it consisted not of one species, but of a group of species. In any case, F. (S.) flori should be regarded not as a direct ancestor of F. (S.) fusca s. s., but as the ancestor of the extended group F. (S.) fusca, which is difficult to distinguish and now comprises no fewer than 6 species, and perhaps also as an ancestor of the F. (S.) rufibarbis group, which separated off quite recently (8).

F. horrida Wheeler was regarded by its author as close to the modern F. (S.) cinerea Mayr, but this conclusion was based upon the extremely strong development of erect pubescence in both forms, a character which cannot be taken into account in this case, since species with such erect pubescence obviously appeared independently and occur in nearly all subgenera. In any case, the Formica chaetotaxy is only a specific character and cannot be used for phylogenetic constructions.

The subgenera Formica + Raptiformica (9) and Coptoformica (16) separated from the subgenus Serviformica at roughly the same time. Characteristic of these is the temporary social parasitism, leading to morphological modifications in the structure of the female: the relative proportions diminish, in the first place, the size of the thorax and abdomen. In Coptoformica, moreover, an emargination appears in the occipital margin of the head and there is tendency towards smoother abbreviation of the maxillary palps, as in Formica + Raptiformica worker polymorphism develops. This form soon divided into the subgenera Formica (10) and Raptiformica. The overwhelming majority of Formica males lost the denticles on the masticatory margin of the mandibles. Complex building instincts developed in this subgenus: the nests of these ants, along with those of the tropical Atta, are regarded as the most intricate nests in the whole ant world. In one or perhaps two of the Raptiformica groups a complicated form of social parasitism developed, resembling "slavery" (15).

The subgenus Formica falls into four groups. Characteristic of the group F. (F.) exsectoides is the presence of an emargination in the occipital margin of the head (13). In species of the F. (F.) microgyna group temporary social parasitism lead to the females' becoming smaller than the large workers (14). In the most extensive group, F. (F.) rufa (12), the nest building instincts and worker polymorphism are more strongly developed than in any of the others. Wheeler (1915) found 2 fossil species of this subgenus, F. (F.) clymene Wheeler and F. (F.) phaethusa Wheeler, which he regarded as closely related to the living species of the F. (F.) rufa group; in particular, he considered F. (F.) phaethusa to be close to F. (F.) truncorum F. The presence of abbreviate maxillary palps in these species, however, as in certain living Coptoformica, precludes assigning them to the subgenus Formica as merely an independently deviate group.

The following stages of morphological evolution can be distinguished in the subgenus Coptoformica: the emargination of the occipital margin becomes deeper and the occipital angles of the head become more acute (17); the female head becomes longer (18); as the result of temporary social parasitism the females do not exceed the size of the workers (19); the maxillary palps become much shorter and the erect hairs are reduced almost all over the body (20).

At present it is impossible to be certain of the subgeneric affinity and phylogenetic links of F. strangulata Wheeler and F. parvula sp. nov.

We can see that the Amber fauna of the Formicini tribe was represented by fairly specialized forms, although the primitive F. (F.) proformicoides sp. nov. persisted. Only one species can be regarded as the direct ancestor of living species, namely, the group F. (S.) fusca – F. (S.) flori Mayr. All the remaining species are obviously lateral branches of evolution.

No specimens which could have been assigned to the subgenera Raptiformica and Coptoformica have as yet been found in the Baltic Amber. This is not surprising in the case of Raptiformica, since the center of differentiation and probably origin of this subgenus was in Nearctia and it is represented by only two species in Palearctica, one of them, F. (R.) sanguinea Latr., very similar to the North American F. (R.) subnuda Em. In regard to the second subgenus, its members inhabit only Palearctica, having two centers of differentiation, one in northern Europe and the other in Mongolia; Coptoformica is therefore very likely to be found in the Baltic Amber.

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